

NOTES ON THE DISTRIBUTION
AND THE SHELL POLYMORPHISM
OF *COCHLICELLA ACUTA* (MÜLLER)
(GASTROPODA, HELICIDAE) IN BELGIUM

by

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1. INTRODUCTION

The distribution of *Cochlicella acuta* (MÜLL.) comprises the littoral zones of the Mediterranean and the coasts of the Atlantic and the southern part of the North Sea. It has been introduced to the Bermuda Islands, South California, California U.S. (PILSBRY, 1939) and Australia (ZILCH & JAECKEL, 1962 ; SMITH, 1970 ; BUTLER & MURPHY, 1977) ; it was recently found in Bulgaria (HUDEC & VASATHO, 1973) and Romania (GROSSU : 1979).

The shell of *Cochlicella acuta* shows a genetically determined polymorphism of the banding, the opacity of the extra-band areas, and the ground colour (LEWIS, 1975, 1976).

This paper deals with the present distribution in Belgium and the geographic variation of the shell polymorphism.

2. MATERIALS AND METHODS

The coastal dune area was intensively searched for *C. acuta* during 1973-1982. The establishment of the most northern colonies was checked in consecutive years.

The relative population density of some 28 colonies (1981 collections), used for shell measurements and shell phenotyping, was determined by sampling a standard area during a standard time (ANDRE, 1973).

The habitats were classified into three types according to LEWIS (1976) :

- Exposed sand : characterized by marram (*Ammophila arenaria* (L.) Link.), tussocks or sparse grass with considerable exposure of sandy substrate.
- Close turf : dense turf or thick grass which covers the substrate.
- Mixed vegetation : all habitats having a coverage of vegetation varying in species composition and density intermediate between the former habitats.

The shell of *C. acuta* has a five-banded system. The bands are numbered 1 to 5, the uppermost being 1 ; absence of bands is indicated by 0 (cf. *Cepaea*). The extra-band areas consist of transverse striae of opaque material with transparent areas between. Shells that are continuously opaque (CO) are distinguished from those that are partly transparent or discontinuously opaque (DO) in the extra-band areas (LEWIS, 1975).

3. RESULTS AND DISCUSSION

3.1. Geographical distribution

Cochlicella acuta was first recorded for Belgium in 1910 (De Panne) by BOULY DE LESDAIN (1911). It was found again at the same locality in 1924, 1927 and 1936 (ADAM, 1947). Empty shells were collected at Nieuwpoort-Bad in 1930 (ADAM, 1947). In 1956 it still did not extend beyond Oostduinkerke, 8 km W from De Panne (DE LEERSNYDER & HOESTLANDT, 1957). In 1960 ADAM mentions the species from De Panne, St. Idesbald, Koksijde and Oostduinkerke.

Our results (Fig. 1) show that in 1973 and up to now *Cochlicella acuta* has an almost continuous distribution between the French border and the river IJzer (Nieuwpoort), where it is to be found in the marram dunes, the dune-pastures and along the roadsides. North of the IJzer only 8 isolated colonies were found (n° 1-8 in Table 1). Colonies 4-8 (Westende and Lombardsijde) were established in 1973 ; colonies 1-3 (Raversijde and Middelkerke) were first recorded in 1981. The most northern colony of the species' range at the east coast of the North Sea lies at 51°12'39" N-2°52'07" E (Raversijde-Bad, Oostende). It is a well established colony located in a dune depression, 325 from OH. This is a spread of some 25 km north in about 70 years since the first record.

The eight isolated northern colonies will further be referred in the text as the marginal populations, e.g. those populations existing at the margin

of the species' geographical range. Seen the isolated character of the marginal populations and their location in sheltered places, protected from sea-winds, it is not impossible that we missed some colonies and that still more northern populations will be found.

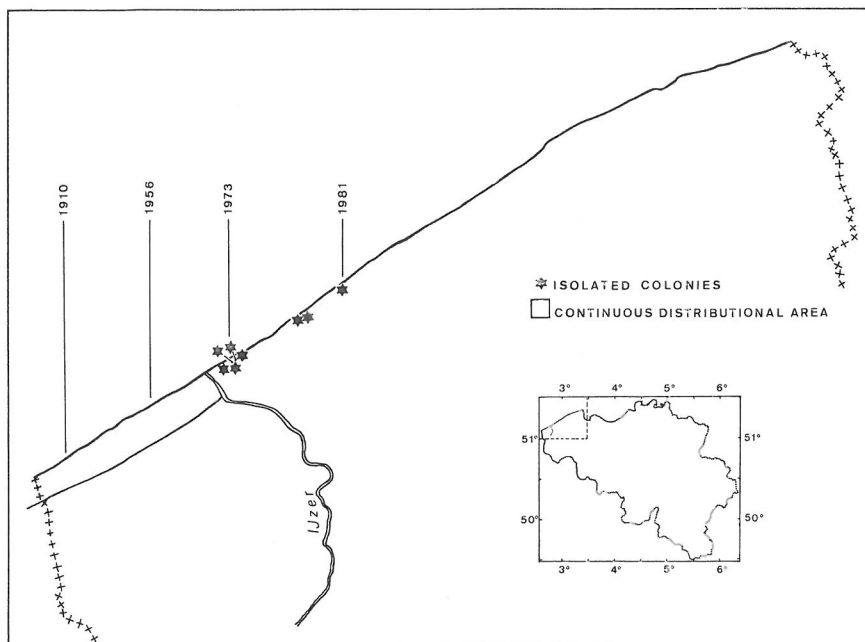


FIG. 1. – Distribution of *Cochlicella acuta* in Belgium.

We attribute the establishment of *C. acuta* in Belgium to the twentieth century climatic amelioration : it is possible that the dispersal coincides with the general rise in mean annual temperature over the northern hemisphere during the early part of the twentieth century (FORD, 1982). Six of the marginal populations are in the vicinity of a parking place, which suggests that man and his car might be an important dispersal agent. The continuous distribution south of the river IJzer shows that the species also knows some active dispersal, and is good evidence that the river acts as a barrier.

3.2. Survey of the life history

The huge majority of *Cochlicella acuta* has an annual lifecycle in the area studied, as illustrated by the unimodal lengthcurves (examples see

Table 1

Collections of Cochlicella acuta : frequency of phenotypes

Locality	Habitat	CONTINUOUSLY OPAQUE			Total	DISCONTINUOUSLY OPAQUE			Total	Total size of sample	
		00300	00340	00040		00300	00340	00040		Unbanded	Banded
1. Raversijde	M.V.	2.42	—	3.64	16.36	—	1.82	12.12.	83.64	165	72.12
2. Middelkerke	C.T.	0.98	—	16.10	17.08	—	—	82.92	82.92	205	99.02
3. Middelkerke	M.V.	22.38	—	45.45	84.61	—	1.40	4.20	15.39	143	67.83
4. Westende	M.V.	56.32	—	2.63	58.95	—	—	1.05	41.05	190	96.32
5. Lombardsijde	C.T.	15.43	3.19	3.72	29.26	—	3.19	5.85	70.74	188	77.13
6. Lombardsijde	E.S.	11.79	0.81	10.57	28.86	1.63	3.66	11.38	71.14	246	66.26
7. Lombardsijde	C.T.	6.25	—	25.00	31.25	—	—	43.75	68.75	16	31.25
8. Lombardsijde	C.T.	44.06	4.99	3.33	93.35	—	—	2.29	6.65	481	48.43
9. Nieuwpoort	E.S.	—	13.33	20.00	33.33	—	—	26.67	66.67	15	40.00
10. Nieuwpoort	C.T.	9.46	—	—	9.46	—	—	8.11	90.54	74	91.89
11. Nieuwpoort	E.S.	33.33	—	22.22	55.55	—	—	11.11	44.44	9	66.66
12. Nieuwpoort	C.T.	5.00	—	5.45	11.37	—	—	39.77	88.64	440	53.86
13. Oostduinkerke	E.S.	9.38	2.83	8.14	24.60	1.06	1.59	26.55	75.40	565	55.58
14. Oostduinkerke	E.S.	9.26	0.62	9.26	23.46	1.85	6.79	10.49	76.54	162	66.67
15. Oostduinkerke	M.V.	54.44	—	11.46	67.91	1.15	1.43	4.58	32.09	349	79.37
16. Oostduinkerke	E.S.	8.31	1.15	6.02	22.06	2.87	3.44	18.91	77.94	349	61.03
17. Oostduinkerke	E.S.	3.11	2.48	4.35	13.04	1.24	2.80	9.63	86.96	322	76.40
18. Koksijde	C.T.	47.98	—	4.62	73.41	—	1.16	8.67	26.59	173	64.74
19. Koksijde	C.T.	—	—	4.16	8.33	—	12.50	4.17	91.67	24	75.00
20. Koksijde	E.S.	22.06	1.07	1.78	32.38	0.36	1.42	8.54	67.62	281	79.36
21. Koksijde	E.S.	4.64	—	1.32	5.96	1.99	—	3.97	94.04	151	92.72
22. St. Idesbald	C.T.	21.28	—	17.02	38.30	—	2.13	8.51	61.70	47	72.34
23. St. Idesbald	E.S.	65.35	—	—	66.34	—	—	—	33.66	101	99.01
24. St. Idesbald	E.S.	43.48	—	3.48	46.96	—	—	6.09	53.04	115	90.43
25. De Panne	E.S.	31.48	—	5.56	37.04	—	—	1.85	62.96	54	92.59
26. De Panne	C.T.	38.46	—	—	38.46	—	—	3.85	61.54	26	96.15
27. De Panne	M.V.	25.76	—	—	25.76	—	—	—	74.24	66	100.00
28. De Panne	M.V.	11.43	—	0.83	12.26	4.99	3.33	42.41	87.74	481	48.44

E.S. : exposed sand ; C.T. : close turf ; M.V. : mixed vegetation.

Fig. 2). The same conclusion was drawn for the species in S.E. England (DE LEERSNYDER & HOESTLANDT, 1957) and the Boulonnais, North of France (DE LEERSNYDER, 1958). However, we found that less than 1 % of the snails last over into the second spring, suggesting that some animals have an expectation of two years (see also AUBERTIN *et al.*, 1930). The main copulation period is September-October, followed by a slight growth increase during November-December and massive mortality of the adults in December. Hatching takes place from December up to and including April.

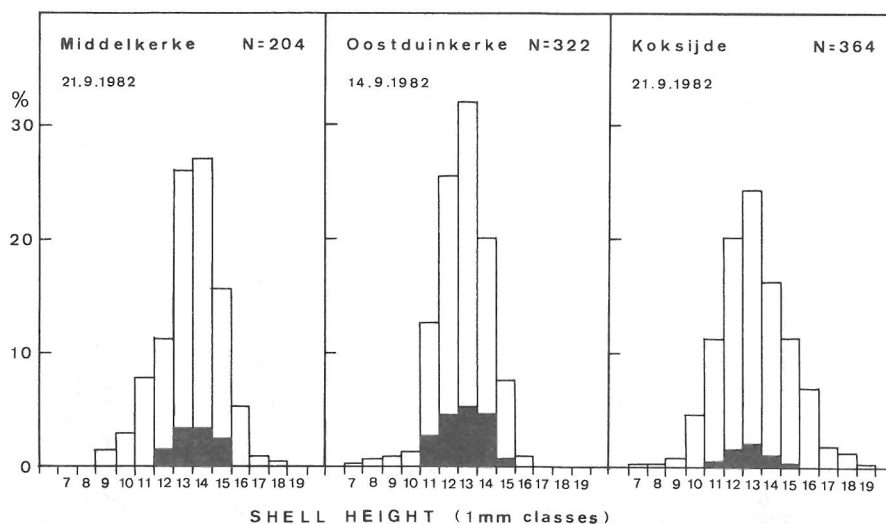


FIG. 2. – Frequency-distribution of shell height in *Cochlicella acuta* from some belgian colonies. In copula individuals black.

3.3. Shell polymorphism

3.3.1. General Survey

A total of 5,438 snails from 28 populations have been studied. The composition of the collections classified by banding and opacity is presented in Table 1 and 2. Fig. 3 shows some main shell phenotypes.

Four banding morphs are found : 00000, 00300, 00340 and 00040. Morphs 00000 and 00040 are to be found in most colonies. The unbanded morph is predominant and accounts for 63.9 % of all snails collected. The one-banded morph 00040 is with 28.9 %, the second most important phenotype ; the frequency of 00300 and 00340 is respectively 2.6 % and 4.6 %. The appearance of band 3 is almost always punctate.

Table 2
*Frequencies of the banding morphs for different
shell opacity in Cochlicella acuta
from the belgian coastal dune region*

Banding	Continuously opaque	Discontinuously opaque	Total
00000	1,122 (20.6 %)	2,354 (43.3 %)	3,476 (63.9 %)
00300	81 (1.5 %)	59 (1.1 %)	140 (2.6 %)
00340	157 (2.9 %)	92 (1.7 %)	249 (4.6 %)
00040	589 (10.8 %)	984 (18.1 %)	1,573 (28.9 %)
Total	1,949 (35.8 %)	3,489 (64.2 %)	5,438 (100 %)

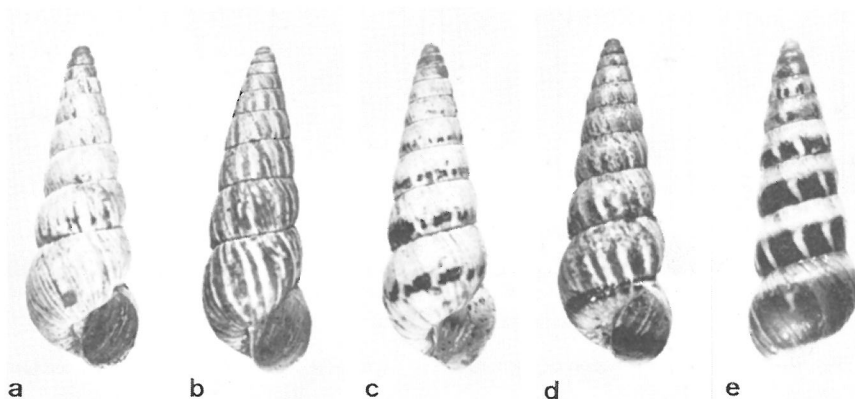


FIG. 3. – Some examples of shell banding and opacity in *Cochlicella acuta*. a : CO 00000 ; b : DO 00000 ; c : CO 00300 ; d : DO 00040 ; e : CO 00(345) (N. France, so far not found in the belgian area).

The discontinuously opaque shells (64.2%) occur more commonly than the continuously opaque ones (35.8%).

3.3.2. Variation in shell polymorphism with habitat

Fig. 4 is a scatter diagram showing the distribution of two classes of phenotypes in the colonies sampled, and the nature of the habitat. The position of a colony is determined by the frequency of CO shells and the percentage of banded shells. Any significant evidence of variation with habitat of opacity and banding is apparently absent (median test). LEWIS

(1976 : 407) has found that, although there is variation in the degree of the relationship, the populations inhabiting close turf are more continuously opaque and more banded than those for mixed vegetation are. He also found that those populations in turn have a greater proportion of individuals that are C.O. and banded than the exposed-sand type ones do. Visual selection by rooks (*Corvus frugilegus*), and some non-visual habitat-related selection, probably microclimatic, would explain the habitat-morph frequency relationship, at least for the heavily banded morphs on dark substrates and for the unbanded, discontinuously opaque and amber ground coloured morph, which has a sandy appearance, on substrates of brown sand (LEWIS, 1975, 1976).

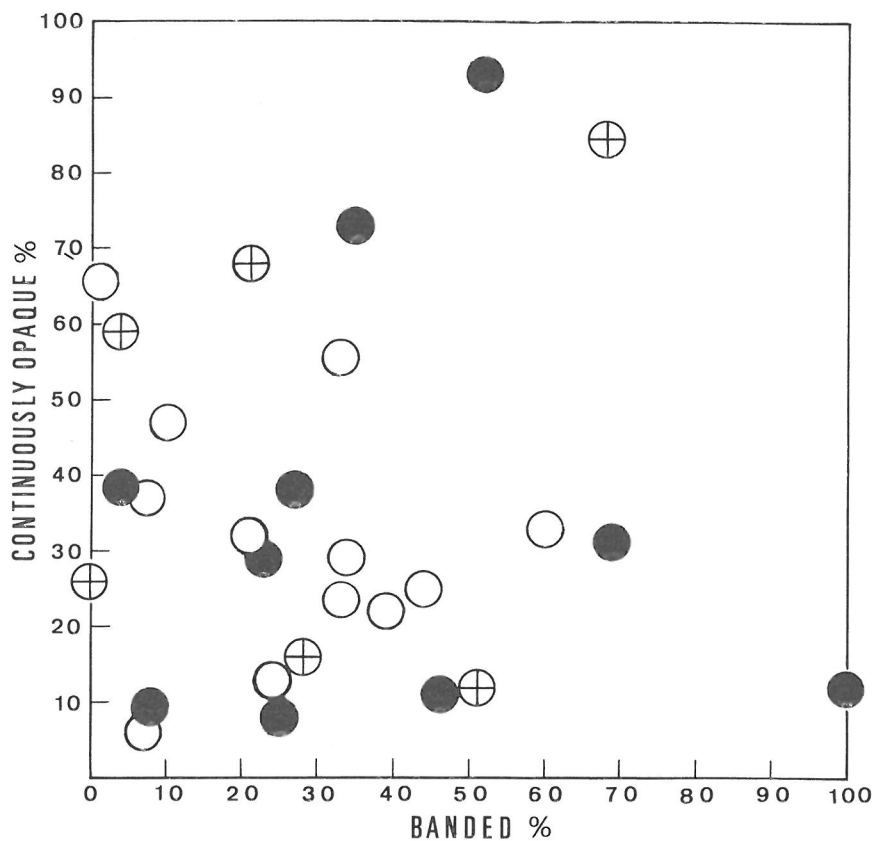


FIG. 4. — Scatter diagram showing the relation between the percentage continuously opaque shells, the percentage of banded shells, and the nature of the habitat for populations of *Cochlicella acuta* from the Belgian area. O : exposed sand, ⊕ : mixed vegetation, ● : close turf.

Our results suggest that visual predatory selection is of little significance or overridden by other selective forces in the belgian populations.

3.3.3. Variation in shell polymorphism with latitude

The colonial frequencies of continuously and discontinuously opaque shells, and their different banding morphs were plotted against latitude for each of the three habitat types. Opacity (continuous or discontinuous), and the phenotypes 00300 and 00340 are independent of habitat and latitude. For the unbanded morph and the banded phenotype 00400 there is strong evidence that the frequency distributions are clinal but independent of habitat (Fig. 5) : the unbanded morph shows a significant decrease with latitude (Spearman's rank correlation coefficient $r_s = -0.501$, $p < 0.0088$), whereas morph 00400 increases with latitude ($r_s = 0.557$, $p < 0.0038$). These clines are most pronounced in the region where the species is widespread (French border – river IJzer). Four of the marginal populations do not follow this general trend (due to their sheltered location ?), which suggests a micro-environmental selection acting on local populations.

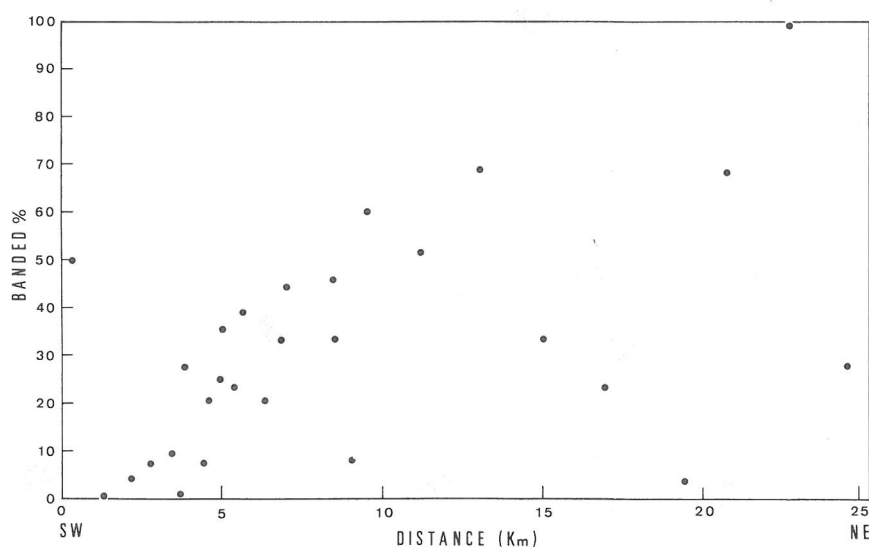


Fig. 5. – Frequency of banded shells in populations of *Cochlicella acuta* along the SW-NE transect of its range in Belgium.

From his survey of about eighty colonies between latitudes 43°N and 58°N in west and northwest Europe (Pyrenees to Outer Hebrides), LEWIS

(1976) found a latitude related selection, strongly acting against the supergene CO 00000 in all types of habitat with increasing northern latitude, and probably due to certain aspects of climate. Our results show that this overall picture of latitude dependent selection for the species' distribution in western Europe, likewise can be brought about over small geographic distances. The pattern of shell banding polymorphism for *Cochlicella acuta* in Belgium seems primarily the result of climatic selection as it parallels a climatic gradient along a SE-NW transect, characterized by an increasing humidity indicated by (Table 3) increases in precipitation, water surplus, humidity index and moisture index, and decreases in accumulated potential water loss, water deficit and aridity index. The cline structure of the shell-banding can possibly be explained physiologically. Snails with pigmented bands will heat up more rapidly to their activity temperature by the absorption of solar energy, and hence are favoured in the wetter environments where cooling by wind action will be higher than in the arid environments. This also holds for morph 00040 as the snails generally take an upside-down position when at rest, thus exposing their bands to direct solar radiation. The unbanded snails will reflect more energy thereby minimizing overheating and desiccation : they are adaptively selected in the warmest and more arid parts of their range. Some of the distributions for colour and banding polymorphism in *Cepaea vindobonensis* (JONES, 1973), *C. nemoralis* (a.o. JONES, 1973 ; JONES *et al.*, 1977 ; ARNOLD, 1969) and *Theba pisana* (NEVO & BAR, 1976) have been found to be correlated with climate in a similar way. Evidence suggesting that climatic factors are of the most important selective forces involved in the distributions of shell polymorphism along the Belgian coastal dune area, was also provided for the Helicidae *Cepaea nemoralis* (DE SMET : 1982), *Theba pisana* and *Cernuella* spp. (in preparation). Field experiments to investigate the implications of climatic selection on *Cochlicella acuta* are conducted in the Zwin area.

3.3.4. The phenotypic diversity

The level of polymorphism estimated by SIMPSON's (1949) diversity index $\lambda = 1 - \sum_{i=1}^s (n_i/N)^2$, which takes into account sample size, the number of phenotypes and their frequency, varies between 0.2199 and 0.7160 ($\bar{\lambda} = 0.5603$). The diversity is independent of latitude, habitat and relative population density. The values of λ for the marginal populations ($\bar{\lambda} = 0.5693$, range 0.2863 – 0.7036) are not significantly different from those of the other populations ($\bar{\lambda} = 0.5567$, range 0.2199 – 0.7160). It thus

follows that *C. acuta* shows no reduction in visual polymorphism at the (northern) limit of its range, a phenomenon which is known to occur for some species (a.o. BOVEY, 1941 ; BANTOCK & PRICE, 1975) so that their marginal populations are sometimes monomorphic.

Table 3

*Mean annual values of climatological data (THORNTHWAITE) *
at the SE and NW range
of Cochlicella acuta in Belgium*

Region	SE	NW
Temperature (°C)	9.5	9.5
Potential evapotranspiration (mm)	640	640
Precipitation (mm)	700	800
Actual evapotranspiration (mm)	600	620
Accumulated potential water loss (mm)	160	130
Water deficit (mm)	40	25
Water surplus (mm)	100	200
Run off (mm)	100	200
Ratio run off/precipitation (%)	15	25
Aridity index I_a	6	4
Humidity index I_h	10	20
Moisture index I_m	20	40
Summer concentration of thermal efficiency	48	49

* After DINGENS & VERNEMMEN (1963).

3.3.5. Variation in shell size

The height of the adult snails, based on *in copula* individuals, varies from 10.0 to 20.0 mm for the species' range in Belgium. Mean shell height for the different populations varies from 11.10 ± 0.92 mm to 16.80 ± 1.48 mm. The adult size is unrelated to habitat (Mann-Whitney U test) neither latitude (r_s), but shows (Fig. 6) a positive correlation with the relative population density ($N = 28$, $r_s = 0.508$, $p < 0.0082$). The regression is given by the equation $y = 10.927 + 0.591 \ln x$ ($r = 0.464$).

Intercolonial variation for shell size in *C. acuta*, without apparent cause, has been recognized by DE LEERSNYDER & HOESTLANDT (1957) and MARCUZZI & GIULINI (1970). The latter suggest a genetic difference instead of a phenotypic origin. In his study on density effects in snails, TATTERSFIELD (1981) reports a significant negative regression of shell size (mean shell height of the populations varying from ± 10.0 mm to

± 12.0 mm) on log density for *C. acuta* given by the equation $y = 11.45 - 0.49 \ln x$ ($N = 8$, $r = -0.709$). He assumes a direct influence of population density on growth rate and processes influencing shell size, possibly mediated by mucus conditioning of the environment, to be the most probable mechanism.

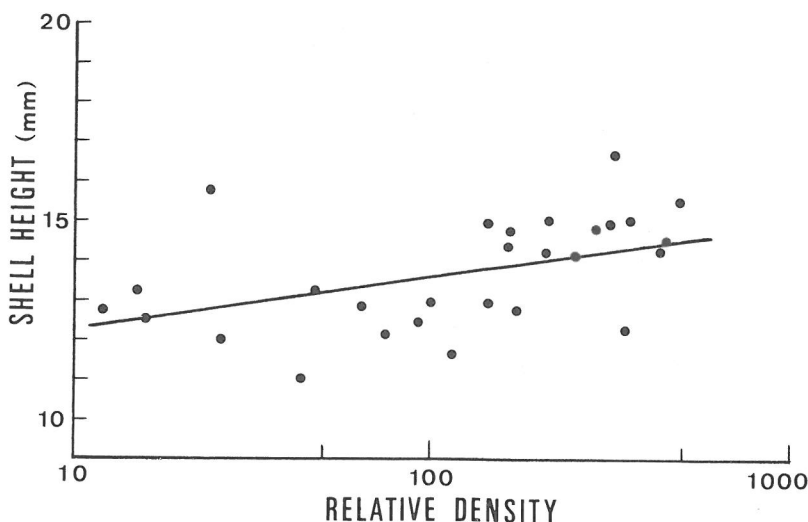


FIG. 6. — Relationship between adult shell height and relative density for *Cochlicella acuta* in the belgian area.

The inverse size/density relationship found for the belgian coastal dune area neither points towards a genetical or behavioural interaction, but probably suggests differences in the availability of high-quality food and consequent differences on either (or in combination) clutch size, juvenile survival and growth rate (BUTLER, 1976 ; EISENBERG, 1966 ; YOM-TOV, 1972). On the other hand might the populations at the northern limit of their range be under any density-dependent control (e.g. climate) restricting population size to a level whereby some kind of chemical conditioning of the environment (THOMAS *et al.*, 1974) by the snails below the critical threshold, resulting in the enhancement of growth and natality rates, could be operating.

SUMMARY

- *Cochlicella acuta* has spread about 25 km north since its first record in Belgium (1910). The dispersal may possibly be attributed to the twentieth century climatic amelioration.

- Associations between shell phenotypes (opacity and banding), and particular habitats could not be demonstrated.
- There is an apparent association between shell banding (and not opacity) and latitude, the selection involved probably being related to climate.
- Shell size shows a positive regression on log density.

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